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FEATURED PAPER

Effect of Pulsed DC Frequency on Capture Efficiency and Spinal Injury of Trout in Small Streams

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Abstract
Electrofishing studies in the 1990s established that higher frequencies of pulsed DC (e.g., 60 Hz) generally result in more spinal injury to fish in comparison with lower pulse frequencies (e.g., 30 Hz). In response to those findings, some agencies adopted low pulse frequency standards to minimize fish injury. However, those earlier studies did not assess whether capture efficiency (CE) was also influenced by pulse frequency. We sampled small trout streams (1–6-m average width; SE = 0.14 m) by backpack electrofishing with settings of 30 and 60 Hz to evaluate the effect of pulse frequency on both CE and spinal injury rates for Cutthroat Trout *Oncorhynchus clarkii*, Rainbow Trout *O. mykiss*, and Brook Trout *Salvelinus fontinalis*. Duty cycle was held constant at 24% and average power output was held at approximately 100 W. Using a four-pass removal protocol, cumulative CE (all four passes) averaged 0.84 for 30-Hz reaches and 0.94 for 60-Hz reaches. Capture efficiency in pass 1 averaged 0.59 for 30-Hz reaches and 0.75 for 60-Hz reaches and declined with successive passes using both pulse frequencies. X-ray images revealed vertebral compressions and misalignments for 4% of fish captured with 30 Hz ($n = 230$) and 4% of those captured with 60 Hz ($n = 222$); no fractured vertebrae were observed. No spinal injuries were observed in control fish that were captured via angling ($n = 92$). Our results indicate that in small streams where trout are generally less than 300 mm TL, backpack electrofishing with 60 Hz will result in greater CE, improved trout occupancy and abundance estimates, and no increase in spinal injury.

Electrofishing is one of the most commonly used methods of assessing fish assemblages and population abundance in lentic and lotic habitats throughout the world. From the 1950s through the 1980s, most electrofishing research was devoted to developing, evaluating, and refining equipment to improve fish capture, and little attention was given to the effect of electrofishing on fish injury. Although early electrofishing injury signals (e.g., Hauck 1949; Spencer 1967) were unheeded, the seminal paper by Sharber and Carothers (1988) documenting high spinal injury rates in large (≥300-mm TL) Rainbow Trout *Oncorhynchus mykiss* by using pulsed DC (PDC) prompted a wave of additional research on factors influencing the severity and rate of electrofishing injury for various fish species.

The proliferation of electrofishing research demonstrated that PDC frequency was one of the most important factors influencing fish injury (e.g., McMichael 1993; Sharber et al. 1994; Dalbey et al. 1996; Ainslie et al. 1998), with frequencies 60 Hz and higher being more injurious. Based on these findings, some state and provincial agencies have established policies or guidelines to limit pulse

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frequency settings in an effort to minimize electrofishing injury, especially for salmonids. For example, the state of Montana requires the use of 30 Hz or less “in any waters containing self-sustaining salmonid populations” (Montana Fish, Wildlife, and Parks 2003). The province of Alberta has a similar policy (Government of Alberta 2012). The National Marine Fisheries Service (NMFS 2000) also recommends 30 Hz for backpack electrofishing and sets a maximum level of 70 Hz for sampling streams “containing salmonids listed under the Endangered Species Act.”

While such policies were being implemented, little research was aimed at the potential influence of pulse frequency on capture efficiency (CE). In small streams containing salmonids, biologists often use backpack electrofishers to make multiple electrofishing passes through a particular study reach and they use the resulting catch data to obtain a maximum likelihood estimate of abundance and CE (Moran 1951; Zippin 1956, 1958). This removal depletion method tends to produce (1) declining fish CE with successive passes and (2) overestimates of CE within each pass, both of which lead to underestimating true fish abundance (e.g., Mahon et al. 1979; Riley and Fausch 1992; Rosenberger and Dunham 2005; Meyer and High 2011). Because the magnitude of the bias in abundance estimates is directly related to the level of bias in CE estimates, maximizing CE inherently improves the precision and accuracy of depletion estimates of fish abundance (Riley and Fausch 1992). Although it is recognized that lower pulse frequencies generally capture fish less readily (Snyder 2003), this has not been formally evaluated. In the present study, we evaluated the effect of low (30-Hz) and high (60-Hz) pulse frequencies on the CE and spinal injury of trout sampled with backpack electrofishing in small streams.

METHODS

Study sites.— We selected 20 streams based on their size and our prior knowledge of trout presence. Because water conductivities are known to affect power transfer to fish (Kolz 1989) and thus may affect CE and fish injury, study streams were selected across the state of Idaho to encompass a range of water conductivities. Sample reaches were established in 1–6-m-wide streams that could be (1) sectioned off effectively with block nets and (2) sampled effectively with one backpack electrofisher. The latter stipulation was to control for the asynchronous effect of multiple electrofishers increasing the pulse frequency in an overlapping electrical field (Beaumont 2017).

Electrofishing surveys were conducted during July–September in 2017 and 2018 after peak streamflows had subsided for the year and before deciduous leaf inputs prevented block nets from functioning effectively overnight. At each stream, two sample reaches (~50 m long) were delineated at the upper and lower ends with double block nets set 1–2 m apart. Block nets (1.2 × 4.6 m) consisted of 1-cm mesh with a floating line along the top and a lead line along the bottom. The floating line was secured to streamside vegetation on either end and propped up in the middle with branches to keep the top of the block nets above water as debris accumulated overnight on the nets. The bottom of the net was secured to the stream bottom by lining it with cobbles and boulders.

Study design and electrofishing procedures.— A Smith-Root LR-24 backpack electrofisher (Smith-Root, Inc., Vancouver, Washington), with a 28-cm-diameter, stainless-steel electrode ring attached to the end of a 1.8-m-long handle and a trailing 3-m-long, braided stainless-steel cable cathode was used for all electrofishing. During electrofishing, the operator moved in an upstream direction and served as the primary netter, while a second person served as a backup netter and carried a bucket for holding captured fish.

When using PDC on the LR-24, pulse frequency, duty cycle, and voltage can be independently manipulated to affect electrofishing performance. To isolate the effects of pulse frequency on CE in this study, it was necessary to standardize other electrofisher settings that could influence CE. The most logical method of doing so was to standardize average power output, which is independent of pulse frequency. Using average power output allows a person simply to observe the backpack unit output display, whereas standardizing by power density requires estimation of electrical field shape and voltage gradient—a more complex method. Average power output is influenced not only by the voltage and duty cycle but also by ambient water conductivity and water depth, among other things. To account for the effects of ambient water conductivity and water depth, prior to any electrofishing we tested the average power output (W) in both pool and riffle habitats that were representative of the depths found within the respective study reach. Duty cycle was held constant at 24%, and voltage was adjusted so that the average output for a pool and riffle reached our desired output (75 W for the marking pass; 100 W for depletion and X-ray passes). Water temperature (°C) and specific conductivity (μS/cm) were measured with an Oakton Cond 6+ conductivity meter (Oakton Instruments, Vernon Hills, Illinois) before and after the marking, depletion, and X-ray passes.

Marking pass.— To empirically determine CE, we first needed to capture and mark fish. For the marking pass, a setting of 30 Hz was used and voltage was adjusted to achieve 75 W of power output averaged across a riffle and pool. This allowed us to capture some fish that reached taxis to the anode, but the conservatively low power output was assumed to elicit minimal fish injury that could confound our subsequent testing of pulse frequency on

CE. Captured fish were measured to the nearest centimeter and given an upper caudal clip for the upstream reach and a lower caudal clip for the downstream reach, with approximately equal numbers of fish marked (generally 10–20) for each reach. After marked fish fully recovered in a bucket of freshwater, they were released into their respective block-netted reaches.

Depletion passes.— Approximately 24 h after the marking pass, we conducted a four-pass depletion in each study reach. Prior to electrofishing, 30- and 60-Hz treatments were randomly assigned to the upper and lower block-netted stream reaches to evaluate the effect of pulse frequency on CE. The operator of the electrofisher was not informed of the pulse frequency treatment being used for that reach, so as not to bias his effort. Although the backup netter did know the settings, the electrofishing operator netted approximately 90% of all fish captured in this study.

We standardized power between the two reaches by testing the output in a riffle and a pool and adjusting the voltage so that power averaged 95–100 W between the two water depths. Power output at or just below 100 W has been observed to result in sufficient fish immobilization (i.e., taxis but not tetany) of trout in small streams (Meyer and High 2011).

During each pass, fish were captured with a dip net and transferred to a bucket of freshwater. At the end of each pass, fish were measured to the nearest centimeter, checked for fin clips, and then placed in a net-pen outside of the sample reach until the four passes were completed. We also electrofished between each set of block nets for all four passes to quantify fish escapement prior to and during the removal process. Escaped fish were recorded for each pass and were removed from subsequent CE analysis.

X-ray analysis.— To specifically evaluate spinal injury rates with 30 and 60 Hz, additional reaches were electrofished outside of the block-netted reaches to ensure that the fish had not been exposed to electrofishing in previous passes. Power output was tested in a riffle and pool as described above and was adjusted to achieve an average of 95–100 W. Twenty fish (10 fish per pulse frequency) were collected using 30 and 60 Hz and were euthanized for subsequent X-ray examination. We also collected and euthanized approximately 10 fish with rod and reel in several streams (outside of the electrofished areas) as a spinal injury control group.

Each trout that was collected for X-ray analysis was kept frozen from the time of field collection until X-ray analysis in the laboratory. X-ray images of dorsal and lateral views were obtained from each individual by using a Sound-Eklin TruDRlx portable digital x-radiography system (Sound Technologies, Carlsbad, California) coupled with a MinXray HF100 + portable X-ray generator (MinXray, Inc., Northbrook, Illinois). Generator settings were approximately 46 kVp (peak kilovoltage) and 2.8 mA but varied slightly depending on the size of the fish. Digital X-ray images from each fish were examined by two readers, neither of whom knew to which treatment the fish belonged. Scores indicating the type of injury, if any, were assigned to each fish in accordance with Reynolds (1996; 0 = no apparent spinal damage; 1 = vertebral compressions; 2 = vertebral misalignments; 3 = vertebral fractures). Disagreements in scores between the two readers were refereed by a third person. The number and locations of affected vertebrae were also noted.

Naturally occurring (congenital) defects, vaguely resembling vertebral compressions, were distinguished from those resulting from electrofishing by assessing the length of the fused vertebrae in addition to the number of rib bones originating from the fused vertebrae. Normally, two rib bones extend from the top and bottom of each vertebra. When spinal compression occurs due to electrofishing, the length of the vertebrae remains constant but the space in between each vertebra is compressed. In a congenital vertebral fusion, the length of the affected vertebrae is often shorter relative to the observed number of ribs originating from the fused vertebrae. As in previous investigations (e.g., Sharber and Carothers 1988, 1990; reviewed by Snyder 2003), such anomalies usually occurred in vertebrae within the caudal peduncle region.

Habitat measurements.— After all electrofishing operations, we collected data on several habitat variables that could affect CE. Five or six equally spaced cross-channel transects were designated for each reach to collect habitat data. Each transect consisted of a 1-m-wide strip of stream area oriented perpendicular to the flow and spanning the width of the stream. At the downstream end of each transect, wetted width and water depth were measured (nearest 0.01 m). Mean depth was calculated by measuring and summing depths at one-fourth, one-half, and three-fourths of the total wetted width and dividing by 4, which accounts for the trapezoidal-shaped cross section of the water (Platts et al. 1983). Substrate composition was estimated within each transect as the proportions of silt (<0.06 mm), sand (0.06–1.99 mm), gravel (2–63 mm), cobble (64–256 mm), boulder (257–4,096 mm), and bedrock (>4,096 mm). Instream wood was quantified as the percentage of the transect occupied by wood over 100 mm in diameter. Overhanging vegetation was measured as the width (m) of vegetation within 2 m of the water surface extending out from the bank into the channel at 0.0, 0.5, and 1.0 m upstream from the transect on each bank. Percent undercut bank, unstable bank, and overhead shade were also visually estimated within each transect. Stream gradient was calculated from differences in elevation of the upstream and downstream ends of the study reaches as obtained from GPS waypoints and topographical maps.

For each of these habitat variables, measurements were averaged among transects to produce means for each reach to be used in the analysis described below.

Data analysis.— Capture efficiency for each reach was calculated as the number of marked fish that were recaptured during each depletion pass divided by the total number of remaining marked fish that were available for capture. The number of marked fish in each reach was estimated from the four-pass removal data (Carle and Strub 1978) by using the FSA package (Ogle 2019) in R (R Core Team 2019). Bias was calculated as $1 - (N_R/N_M)$, where N_R is the number of marked fish estimated using the Carle–Strub removal depletion estimator and N_M is the known number of marked fish in each reach.

To assess factors that affected fish capture, a mixed-effects cumulative logit model of the odds of recapturing marked fish in each pass was performed using the "ordinal" package (Christensen 2019) in R (R Core Team 2019). This model is written as

$$\log_e\left(\frac{P(Y_i \leq j)}{1 - P(Y_i \leq j)}\right) = \theta_j - x_i\beta,$$

where $P(Y_i \leq j)$ is the probability (Y) that a marked fish was captured during a pass ($\leq j$), θ is the intercept for that pass, x is a vector of explanatory variables for the ith observation, and β is the corresponding set of regression parameters. Marked fish that were not recaptured were assigned a pass number 5, and the probability of these occurrences was simply $1 - P(Y_i \leq j)$. Models were built to assess factors of interest that we hypothesized would affect the capture of marked fish, including pulse frequency (Hz), ambient water conductivity (μS/cm), water temperature (°C), fish species, stream gradient (%), boulder and cobble substrate (combined; %), fish TL (cm), average power output (W), stream depth (cm), overhead stream shading (%), undercut bank (%), overhanging vegetation width (m), and large wood (%). Specific conductivity was converted to ambient conductivity for analysis because it influences electrical current, power output, and, potentially, CE (Reynolds and Kolz 2012).

The aforementioned factors were modeled as fixed effects, whereas stream was included as a random effect with varying intercepts. Candidate models were ranked using Akaike's information criterion (AIC; Burnham and Anderson 1998), and models having an AIC difference (ΔAIC) value no greater than 2 were considered most plausible (Burnham and Anderson 2004). Model coefficients and 95% confidence intervals are reported for the top-three candidate models.

Scores from X-ray analysis were grouped into either injured (score = 1, 2, or 3) or not (score = 0; Reynolds 1996). A chi-square analysis (α = 0.05) was performed to compare the rates of injury between fish captured with 30 Hz and those captured with 60 Hz.

RESULTS

The surveyed stream reaches varied considerably in mean wetted width (1.6–5.2 m), water temperature (5.9–16.1°C), ambient conductivity (41–357 μS/cm), and physical habitat characteristics (Table 1). In total, 639 trout were marked among all reaches, ranging in size from 9 to 29 cm; individual reaches contained 9–21 marked fish. During the four-pass removals, 1,261 total fish were captured, 561 of which were marked recaptures. Sampled trout species consisted of Brook Trout *Salvelinus fontinalis* (N = 236), Rainbow Trout (N = 195), and Cutthroat Trout *O. clarkii* (N = 208). Twenty-three individuals escaped from the reaches and were recovered between the double block nets; these fish were therefore excluded from the data analysis. Power output during removal estimates averaged 99.4 W across riffles and pools at all sites, and the voltage needed to achieve the desired output (in conjunction with a 24% duty cycle and the respective pulse frequency) averaged 385 V (range = 215–775 V) in 30-Hz reaches and 386 V (range = 215–775 V) in 60-Hz reaches.

Cumulative CE was 0.84 for 30-Hz reaches and 0.94 for 60-Hz reaches. In reaches sampled with 30 Hz, CE averaged 0.59 on pass 1, 0.39 on pass 2, 0.19 on pass 3, and 0.16 on pass 4. In reaches sampled with 60 Hz, CE averaged 0.76 on pass 1, 0.59 on pass 2, 0.42 on pass 3,

TABLE 1. Physicochemical characteristics of the 40 reaches in 20 Idaho streams that were electrofished for trout.

Variable	Mean	Variance	Range
Reach length (m)	55.7	432.7	32–142
Temperature (°C)	12.3	5.7	5.9–16.1
Specific conductivity (μS/cm)	209	15,155	53–443
Ambient conductivity	170	8,945	41–357
Mean width (m)	3.0	0.8	1.6–5.2
Mean depth (cm)	12.2	0.2	5–24
Gradient (%)	3.6	0.1	1.4–8.1
LWD (%)	4.8	0.1	0.0–33.0
Undercut bank (%)	14.6	0.3	0.0–50.0
Overhead shading (%)	36.3	0.6	1.0–96.0
Overhanging vegetation (m)	0.3	0.1	0.0–0.8
Unstable bank (%)	12.9	0.3	0.0–50.0
Substrate (%)			
Fines	9.5	0.2	0–27
Sand	9.3	0.2	0–28
Gravel	29.4	0.5	13–55
Cobble	34.3	0.6	8–58
Boulder	17.5	0.4	0–50
Bedrock	0.0	NA	NA

and 0.15 on pass 4. Larger fish were generally captured in the earlier passes for both pulse frequencies (Figure 1). Bias in the estimated number of marked fish averaged −0.16 for the reaches sampled with 30 Hz and −0.06 in reaches sampled with 60 Hz (Figure 2).

According to the most plausible model, which included pulse frequency, fish TL, water temperature, and water depth (Table 2), the odds of recapturing a marked fish by using 60 Hz were 2.24 (i.e., $\frac{1}{0.446}$) times that of recapturing a marked fish by using 30 Hz (Table 3). In addition, for every 1-cm increase in TL, the odds of marked-fish recapture increased by a factor of 1.19 (i.e., $\frac{1}{0.841}$; Table 3). Water depth had a negative effect on recapture odds, which decreased by a factor of 0.92 (i.e., $\frac{1}{1.082}$) for every 1-cm increase in depth (Table 3). Water temperature and ambient water conductivity were among the variables included in the top three models, and thus they contributed to variation in recapture probability; however, the confidence intervals of their exponentiated model coefficients overlapped 1.0, suggesting no effect. Capture probabilities predicted with the top model at mean depth, temperature, fish TL, and conductivity were higher for 60 Hz than for 30 Hz, particularly on the first pass (Figure 3).

In total, 571 trout were collected for X-ray analysis, including 243 fish captured by using 30 Hz, 235 captured with 60 Hz, and 93 captured via angling. Images of 26 fish were discarded due to poor image resolution. Of the remaining 230 trout that were sampled with 30 Hz and used for X-ray analysis, 4% (9 fish) had vertebral compressions or misalignments. Of the remaining 222 fish that were sampled with 60 Hz and used for X-ray analysis, 4% (9 fish) had vertebral compressions or misalignments. No significant difference in spinal injury rate was observed between the 30-Hz and 60-Hz groups ($\chi^2 = 1.66 \times 10^{-29}$, df = 1, $P = 1.00$). Larger fish were not more prone to injuries, with injured fish averaging 13 cm TL compared with 17 cm TL on average for uninjured fish. Among the 93 angled fish, none exhibited spinal injuries. No fractured vertebrae (score = 3) were observed in any fish from any of the treatments. Congenital defects were also rare, occurring in 4% of angled fish, 2% of 30-Hz fish, and 1% of 60-Hz fish.

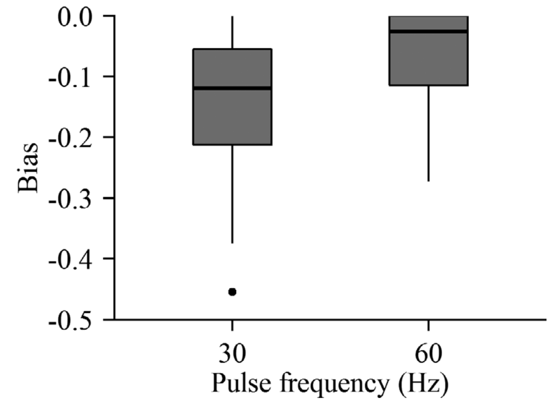

FIGURE 2. Bias in abundance estimates of marked trout in streams that were electrofished by using a pulse frequency of 30 or 60 Hz. Bias was calculated as $1 - (N_R/N_M)$, where N_R is the number of marked fish estimated using a Carle–Strub removal depletion estimator and N_M is the known number of marked fish.

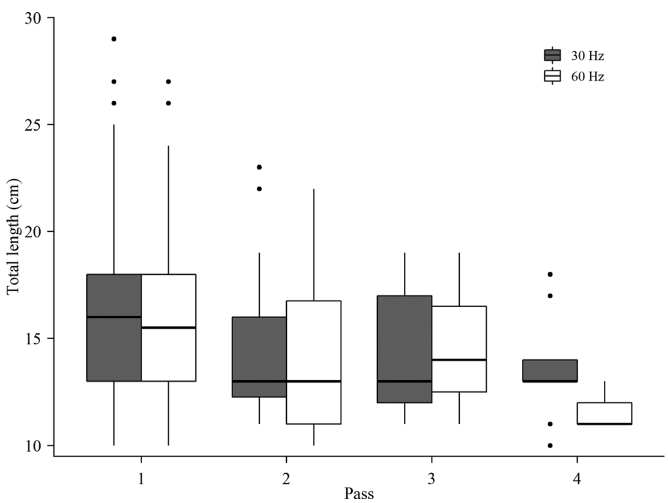

FIGURE 1. Box plot showing the total length (cm) of marked trout that were recaptured in each pass of the four-pass removal by using electrofishing at a pulse frequency of 30 or 60 Hz. The boxes show the interquartile ranges (IQR, first to third quartiles); the line within the box denotes the median; the whiskers extend to 1.5× IQR (or to minimum/maximum values); and the dots represent outliers of fish lengths.

DISCUSSION

Numerous factors affect fish CE during stream electrofishing, with fish size (larger fish are immobilized more readily), stream channel complexity (increased complexity decreases CE), electrical waveform (AC, DC, or PDC), electrical intensity of shocker settings (i.e., power output, amperage, voltage, and duty cycle), and experience of the crew conducting the survey often being important (reviewed by Reynolds and Kolz 2012). Pulse frequency has been shown to be a primary driver in electrofishing-related injury (McMichael 1993; Sharber et al. 1994; Dalbey et al. 1996; Ainslie et al. 1998), but prior to our study the influence of pulse frequency on CE had not been evaluated. We found that CE was significantly higher at 60 Hz than at 30 Hz, suggesting that at higher pulse frequencies, fish tend to be immobilized more quickly and intensely, resulting in easier capture and less bias in depletion abundance estimates.

The greatest disparity in CE between 30 and 60 Hz was during the first pass, suggesting that the benefit of using a higher pulse frequency occurs primarily during the fish's

TABLE 2. Comparison of mixed-effects cumulative logit models relating electrofisher, fish, and stream variables to the odds of capturing previously marked trout. Degrees of freedom (df), Akaike's information criterion (AIC_c), AIC_c difference (ΔAIC_c), and AIC_c weight (ω) were used to select the most plausible models (i.e., models with ΔAIC_c values ≤ 2.0) from a set of candidate models. Pulse frequency (Hz) was either 30 or 60 Hz; fish TL (cm), water temperature (°C), water depth (cm), ambient water conductivity (μS/cm), boulder substrate (%), overhead shading (%), substrate (% cobble + boulder), undercut bank (%), gradient (%), overhanging vegetation (m), and average power output (W) were continuous variables. Ambient water conductivity was scaled to a standard normal distribution. Stream was included as a random effect in all candidate models.

Model	df	AIC_c	ΔAIC_c	ω
$P(Y_i \le j) = \exp$(Intercept − Hz − Fish TL − Depth − Temperature)	9	1,047.6	0	0.300
$P(Y_i \le j) = \exp$(Intercept − Hz − Fish TL − Depth)	8	1,047.6	0.02	0.297
$P(Y_i \le j) = \exp$(Intercept − Hz − Fish TL − Depth − Conductivity)	9	1,048.3	0.66	0.216
$P(Y_i \le j) = \exp$(Intercept − Hz − Fish TL − Depth − Conductivity − Shade)	10	1,050.3	2.72	0.077
$P(Y_i \le j) = \exp$(Intercept − Hz − Fish TL − Temperature)	8	1,051.1	3.47	0.053
$P(Y_i \le j) = \exp$(Intercept − Hz − Fish TL − Depth − Temperature − Species)	11	1,051.3	3.67	0.048
$P(Y_i \le j) = \exp$(Intercept − Hz − Fish TL)	7	1,054.9	7.25	0.008
$P(Y_i \le j) = \exp$(Intercept − Hz − Fish TL − Species)	9	1,058.7	11.11	0.001
$P(Y_i \le j) = \exp$(Intercept − Fish TL)	6	1,074.5	26.93	0.000
$P(Y_i \le j) = \exp$(Intercept − Hz − Depth)	7	1,078.7	31.12	0.000
$P(Y_i \le j) = \exp$(Intercept − Hz)	6	1,083.6	35.94	0.000
$P(Y_i \le j) = \exp$(Intercept − Hz − Species)	8	1,087.6	40.00	0.000
$P(Y_i \le j) = \exp$(Intercept − Depth)	6	1,091.6	43.96	0.000
$P(Y_i \le j) = \exp$(Intercept − Boulder)	6	1,099.0	51.37	0.000
$P(Y_i \le j) = \exp$(Intercept − Shade)	6	1,101.2	53.59	0.000
$P(Y_i \le j) = \exp$(Intercept − Temperature)	6	1,101.8	54.17	0.000
$P(Y_i \le j) = \exp$(Intercept)	5	1,102.4	54.79	0.000
$P(Y_i \le j) = \exp$(Intercept − Conductivity)	6	1,102.5	54.84	0.000
$P(Y_i \le j) = \exp$(Intercept − Substrate)	6	1,103.6	55.99	0.000
$P(Y_i \le j) = \exp$(Intercept − Undercut bank)	6	1,103.9	56.33	0.000
$P(Y_i \le j) = \exp$(Intercept − Gradient)	6	1,104.2	56.62	0.000
$P(Y_i \le j) = \exp$(Intercept − Vegetation)	6	1,104.4	56.74	0.000
$P(Y_i \le j) = \exp$(Intercept − Watts)	6	1,104.4	56.81	0.000
$P(Y_i \le j) = \exp$(Intercept − Species)	7	1,106.4	58.82	0.000

initial encounter with electricity. Subsequent exposure to electricity could result in either avoidance behavior or physical trauma in the uncaptured fish—both of which would explain a decrease in catchability with each pass. In addition, the fish that were largest and therefore most susceptible to capture were typically removed during the first pass, which also contributed to lower CE in subsequent passes. Declining CE with each pass is a violation of the depletion estimator assumption of equal catchability among passes. Although some estimators can test for unequal catchability given a sufficient number of passes (White et al. 1982), the result of this assumption violation is typically an underestimate of true abundance compared to mark–recapture methods (Rosenberger and Dunham 2005; Meyer and High 2011).

Although CE was higher for 60 Hz than for 30 Hz, no corresponding increase in injury rate was observed at the higher pulse frequency, contrary to our expectations. Indeed, the overall spinal injury rate we observed (4%) was much lower than has generally been reported in previous studies of electrofishing injury for stream-dwelling salmonids. However, most previous reports of higher injury rates (i.e., 25–50%) were from investigations in large rivers with boat electrofishers capturing larger (>250-mm) salmonids (e.g., Holmes et al. 1990; Sharber et al. 1994; Dalbey et al. 1996; McMichael et al. 1998). In small streams with backpack electrofishers, previous studies have found spinal injury rates that are more comparable to ours, such as 1–5% for small Rainbow Trout (McMichael et al. 1998) and 15% for Brook Trout (Hollender and Carline 1994). This disagreement in injury rates suggests that pulse frequency may disproportionately influence fish injury with more powerful units commonly used in larger waters. Our results suggest that in small streams sampled with single backpack electrofishers, biologists can benefit from greater CE (i.e., more accurate abundance estimates) associated with 60 Hz without an increase in spinal injury for salmonids.

Besides the influences of fish size, pulse frequency, and stream depth on CE, we found little evidence of other characteristics affecting CE in our study streams. This contrasts with previous backpack electrofishing studies in small streams, which have demonstrated lower salmonid

TABLE 3. Mixed-effects cumulative logit model coefficients, their estimates (exponentiated), and 95% confidence intervals (CIs) for the top candidate models relating electrofisher, fish, and stream variables to the capture efficiency of electrofished trout (Hz = pulse frequency). Ambient water conductivity was scaled to a standard normal distribution. Stream was included as a random effect in all models.

Coefficient	Estimate	95% CI
$P(Y_i \leq j) = \exp(\text{Intercept} - \text{Hz} - \text{Fish TL} - \text{Depth} - \text{Temperature})$		
Intercept (pass 1)	0.098	0.010–0.956
Intercept (pass 2)	0.272	0.023–2.212
Intercept (pass 3)	0.344	0.035–3.367
Intercept (pass 4)	0.430	0.044–4.225
Pulse frequency (60 Hz)	0.446	0.301–0.660
Fish TL (cm)	0.841	0.791–0.894
Water depth (cm)	1.082	0.010–0.149
Water temperature (°C)	0.908	0.806–1.023
$P(Y_i \leq j) = \exp(\text{Intercept} - \text{Hz} - \text{Fish TL} - \text{Depth})$		
Intercept (pass 1)	0.446	0.127–1.561
Intercept (pass 2)	1.033	0.295–3.618
Intercept (pass 3)	1.569	0.446–5.519
Intercept (pass 4)	1.964	0.556–6.937
Pulse frequency (60 Hz)	0.464	0.314–0.685
Fish TL (cm)	0.842	0.791–0.896
Water depth (cm)	1.108	1.038–1.183
$P(Y_i \leq j) = \exp(\text{Intercept} - \text{Hz} - \text{Fish TL} - \text{Depth} - \text{Conductivity})$		
Intercept (pass ≤ 1)	0.459	0.133–1.587
Intercept (pass ≤ 2)	1.063	0.307–3.677
Intercept (pass ≤ 3)	1.614	0.464–5.607
Intercept (pass ≤ 4)	2.020	0.579–7.048
Pulse frequency (60 Hz)	0.461	0.312–0.681
Fish TL (cm)	0.843	0.793–0.897
Water depth (cm)	1.107	1.038–1.181
Water conductivity (μS/cm)	0.828	0.610–1.122

CE with higher channel complexity in the form of cobble–boulder substrate, instream wood, stream shading, and undercut banks (Kennedy and Strange 1981; Peterson et al. 2004; Rosenberger and Dunham 2005; Meyer and High 2011). This disparity suggests that any influence of channel complexity on CE can be mediated or outweighed by other factors, depending on the combination of electrical output and fish sampled.

Our use of 100-W average power at all water conductivities encountered during the study is contrary to power transfer theory as applied to electrofishing (Kolz 1989). The theory requires that power output be adjusted based on the difference between water conductivity and fish conductivity. However, the 100-W standard was apparently successful because (1) salmonids are particularly vulnerable to electrofishing and (2) the shallow depths of small streams compress the electric field to achieve effective intensities (e.g.,

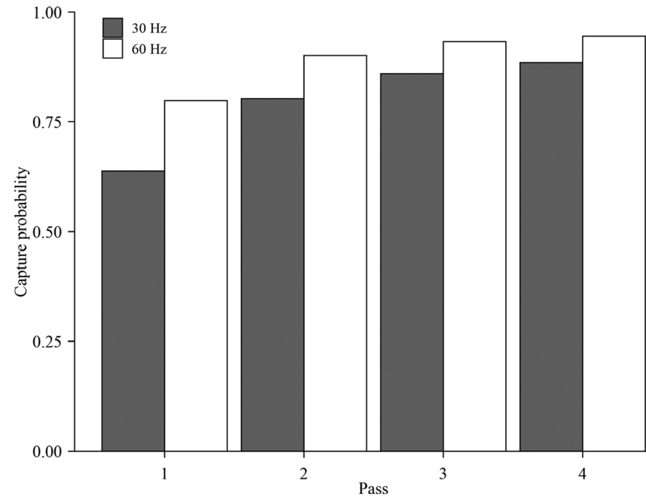

FIGURE 3. Cumulative predicted capture probabilities of marked trout during four-pass removal. The model used included a categorical factor of pulse frequency (Hz) and mean values of three continuous variables: fish TL (cm), water temperature (°C), and water depth (cm).

power density, $\mu W/cm^3$) regardless of water conductivity. Even though power density was functionally responsible for power transfer from the water to the fish during our sampling, it would have been unreliable to use in the field under varying habitat conditions. Using average power—measured directly from circuit metering as a surrogate for power density—was a more reliable standard. At higher conductivities, 100 W might have been less effective, but further tests would be necessary for clarification.

While these conclusions are encouraging for users of backpack electrofishing as a sampling tool, they do have limitations. In larger wadeable streams requiring multiple backpack electrofishers, overlapping of the electrical fields may result in pulse frequencies that are higher than the settings of individual units (Beaumont 2017), perhaps leading to higher rates of injury. Furthermore, we standardized the average power output at 100 W, and our results may not apply to backpack electrofishing operations or boat-mounted systems using higher power output. Finally, our study involved only salmonids; therefore, until additional taxa are evaluated we can only speculate on the applicability of our findings to other fishes. Nevertheless, our results clearly demonstrate that in small streams where a single backpack electrofisher is adequate to capture salmonids, the use of 60 Hz will improve CE and therefore fish occupancy and abundance information without injuring a greater number of fish than would be injured at lower pulse frequencies. Consequently, we recommend that users of backpack electrofishers weigh the benefits of more accurate CE data at higher pulse frequencies with the understanding that they are likely not injuring more fish. We encourage similar evaluations on various species to determine the extent to which higher pulse frequencies can be used. Electrofishing operators should also consider that even with the possibility of higher injury rates for larger fish or with higher power output settings, population-level effects should not be a concern because of the small proportion of fish that are sampled in typical riverine electrofishing surveys (Schill and Beland 1995).

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